RECOGNITION OF BOLTONIA ASTEROIDES VAR. GLASTIFOLIA AND REESTABLISHMENT OF A MORE RESTRICTIVE TAXONOMIC CONCEPT FOR BOLTONIA ASTEROIDES VAR. ASTEROIDES

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ABSTRACT

Recent studies of field and herbarium material indicate that *Boltonia asteroides* var. glastifolia (Hill) Fern. is a distinctive taxon as outlined by Fernald (1940). Several morphological characters and distinctively different habitats separate this taxon from the more insular *Boltonia asteroides* var. asteroides, a taxon known only from the Susquehanna River in Pennsylvania and Maryland. An epitype is designated for var. glastifolia.

KEY WORDS: epitype, Matricaria glastifolia, Boltonia asteroides var. asteroides, Boltonia asteroides var. glastifolia

Boltonia asteroides (L.) L'Her.was the first species to be recognized in the genus now known as Boltonia, being described by Linnaeus (1767) from Pennsylvania material sent by William Bartram. This species was originally placed in the genus Matricaria by Linnaeus, as was Matricaria glastifolia Hill, another American species named just two years later (Hill 1769). L'Heritier de Brutelle (1788) subsequently transferred these two species to the genus Boltonia due to the morphological differences seen between this exclusively American genus and Matricaria.

Fernald (1940) was the next to seriously investigate the taxonomy of this genus, prompted by identification problems he encountered during field work in southeastern Virginia. His range-wide treatment included investigation of the Linnaean type of *Matricaria asteroides* L. as well as the original plate of *Matricaria glastifolia*. His experience in the field and herbarium indicated the presence of two southeastern taxa in this complex, and he used this original material to build his case for their separation and the application of names. Although he did not think they deserved species status, they were nevertheless different taxa with apparently available names. He published the new combination *Boltonia asteroides* var. *glastifolia* (Hill) Fern. (Fernald 1940) to call attention to the coastal plants he had encountered in southeastern Virginia.

Application of the epithet *glastifolia* within the genus *Boltonia* has been inconsistent at best, and specimens from the 1800's and early 1900's seem as likely to bear one name as the other. Morgan (1966) chose not to recognize var. *glastifolia*, stating that the plants so named "...did not differ enough from the species to warrant taxonomic recognition," but no further discussion or data was provided to support this conclusion. Anderson (1987) did not mention this name in his paper describing a new species in the genus (*Boltonia appalachicolensis* L.C. Anderson), even though he discusses other varieties of *B. asteroides*. In the vast majority of recent cases, the name *glastifolia*, no matter its rank, has been ignored by botanists.

While studying herbarium specimens as part of a related taxonomic problem in *Boltonia* (description of a new species, *Boltonia montana* Townsend & Karaman-Castro; Townsend & Karaman-Castro 2006), particular attention was paid to varieties *asteroides* and *glastifolia* as circumscribed by Fernald (1940) and their distinctness was apparent. Differences in plant stature,

means of perennation (stolons vs. basal "offsets"), leaf shape, culm dimensions, and inflorescence details, among others, support the recognition of var. asteroides and var. glastifolia as separate infraspecific taxa.

Due to the original focus of this project on the then-unnamed *montana* entity, herbaria having an appropriate geographical emphasis were targeted for loans (Boltonia montana only known from certain mid-Atlantic states). When specimens of the glastifolia taxon and B. asteroides var. asteroides were sent as part of the loan, attention was paid to these taxa as well. Investigations were soon undertaken into glastifolia morphology due to some seemingly distinctive characters and its almost universal relegation to synonymy under B. asteroides. Keeping in mind the original focus on B. montana, morphological data presented in this paper are based on holdings at BKL, GH, NY, PH, and selected specimens from GA, MO, and LSU. The latter three institutions were investigated at the suggestion of Dr. Vesna Caraman-Castro, eventual co-author of B. montana. The herbarium of the Virginia Department of Conservation and Recreation's Division of Natural Heritage was also consulted. Certain specimens at VPI and NCU were also examined at length but did not contribute to the measurements included in the Morphology section of this paper.

Discussion

Fernald (1940) contended that the original material and description (Hill 1769; illustration: Tab. 3, description: p. 19) of Matricaria glastifolia was representative of the strongly stoloniferous, taller taxon Fernald knew from the outer coastal plain of Virginia and not the plant Linnaeus described from Bartram's Pennsylvania material. Inspection of the same plate does show a resemblance to the stoloniferous coastal plant, with leaves somewhat unlike Linnaeus' asteroides from the Susquehanna. In particular, the more pointed leaf apices, attenuated leaf bases, and the reduction in leaf size from just below the inflorescence upward are consistent with B. glastifolia as interpreted by Fernald and as treated in this paper. The main shortcoming of the illustration is the lack of lower stem details; the long stolons and any remaining lower leaves are not illustrated. Hill's accompanying Latin diagnosis is fairly brief and does not provide any outstanding characteristics to help singularly identify the plant.

The epithet glastifolia apparently refers to "glastum" or "dyers woad", a common name for Isatis tinctoria L. (Brassicaceae), a plant originally of the Caucasus, Asia, and Siberia but cultivated in Europe since ancient times and heavily traded for its blue dye (Roberts 2013). Cultivation has since spread it to other areas of the globe, including North America. This plant has basal leaves narrowed to petiolar bases and culm leaves acute with strongly sagittate bases. Although the culm leaves of var. glastifolia are not sagittate (nor are leaves of any other species in the genus), they are noticeably acute and oriented upwards as in *Isatis*. The basal leaves of *Isatis* in particular are quite similar to those of the coastal *Boltonia* in that they have a relatively wide blade but are narrowed to definite petiolar bases. This character would have been more obvious during cultivation at Kew (where the type illustration was drawn) but not in the wild, where these leaves are usually deciduous by flowering time. The tendency to have such petiolar leaves does extend up the stem at times, with the leaves nearest the basal portion of the plant expressing this character the most. Other species given the epithet glastifolia exist, with an excellent example being the European "Woad-leaved Centaurea" (Centaurea glastifolia L.). Again, the plant has basal leaves strongly narrowed to petioles and the upper leaves are narrow and definitely acute.

Fernald's concept of the glastifolia taxon is encapsulated in this quote from his 1940 revision of the genus:

"Near the coast, on muddy shores or in tidal marshes (see p. 396) from southern New Jersey to Louisiana, Boltonia asteroides becomes stiffer, with firmer leaves and taller stems, and with more promptly stoloniferous habit. In this plant the principal leaves are narrowed into petiolar bases and the stiffer and straighter peduncles are often more bracteolate".

His examination of a photograph of the type specimen of Matricaria asteroides from the Linnaean Herbarium, on the other hand, showed a different morphology. The image matched the specimens from the Susquehanna River Fernald had examined, and was different from the more widely distributed plant of the Atlantic and Gulf coastal plains (var. glastifolia). He briefly described the basic differences between the typical variety and var. glastifolia, providing an image of one of his collections (M.L. Fernald 11,466) and a list of other typical specimens (Fernald 1940).

Fernald's quote alludes to problems with the type illustration of Matricaria glastifolia, which only captures the uppermost portion of the plant and does not show many of the details so important in identifying plants in this rather technical genus (details of involucral bracts, seeds, clonal organs, flower color, etc.). Even with the accompanying latin, a connection between the original material and modern day specimens cannot be made with absolute certainty. For instance, Fernald (1940) justified use of the name glastifolia by saying:

"Some specimens of this coastwise plant are a good match (taking into account the fact that it had been in cultivation) for the original plate of Matricaria glastifolia Hill, basinym of B. glastifolia (Hill) L'Her."

The wording of this statement alludes to the ambiguity of the type material. Such a situation necessitates further action if this name is to be firmly linked to the presumably intended taxon of the southeastern coastal plain. Designation of an epitype in this situation would be an appropriate way to rectify problems with the original material, thus clarifying the use of the name glastifolia. The International Code of Nomenclature (McNeil et al. 2013; Article 9.8) describes an epitype as this:

"... a specimen or illustration selected to serve as an interpretative type when the holotype, lectotype, or previously designated neotype, or all original material associated with a validly published name, is demonstrably ambiguous and cannot be critically identified for purposes of the precise application of the name of a taxon."

In order to clarify the morphological bounds of the var. glastifolia, Fernald's collection number 11,466 at NY (duplicates at PH and GH) is selected to serve as the epitype of Matricaria glastifolia. A photograph of Fernald's 11,466 at GH was the image of var. glastifolia Fernald included in his 1940 paper arguing for its recognition, therefore making it an appropriate collection to help solidify use of the name. The specimen at NY was chosen since it seems to show the most typical morphology of the three available specimens.

MATRICARIA GLASTIFOLIA Hill, Hortus Kewensis, p. 19, tab. 3. 1769. Boltonia glastifolia (Hill) L'Her., Sertum Anglicum 27. 1788. Boltonia asteroides var. glastifolia (Hill) Fern., Rhodora 42: 486. 1940. TYPE: (the entire protologue is this): "Caulis tripedalis ramosus, subdichotomus; geniculis paululum intumescentibus. Folia lanceolata, sessilia, integerrima. Corollae radii purpurascentes. Perennis. Ex America boreali. Augusto florens." (holotype: tab. 3 in Hill 1769). EPITYPE (designated here): USA. Virginia. James City Co.: Fresh tidal marsh of Chickahominy River, below Barratt's Bridge (or Ferry), 19 Sep 1939, M.L. Fernald 11466 with B. Long (NY, Fig. 1; duplicates: GH, PH).

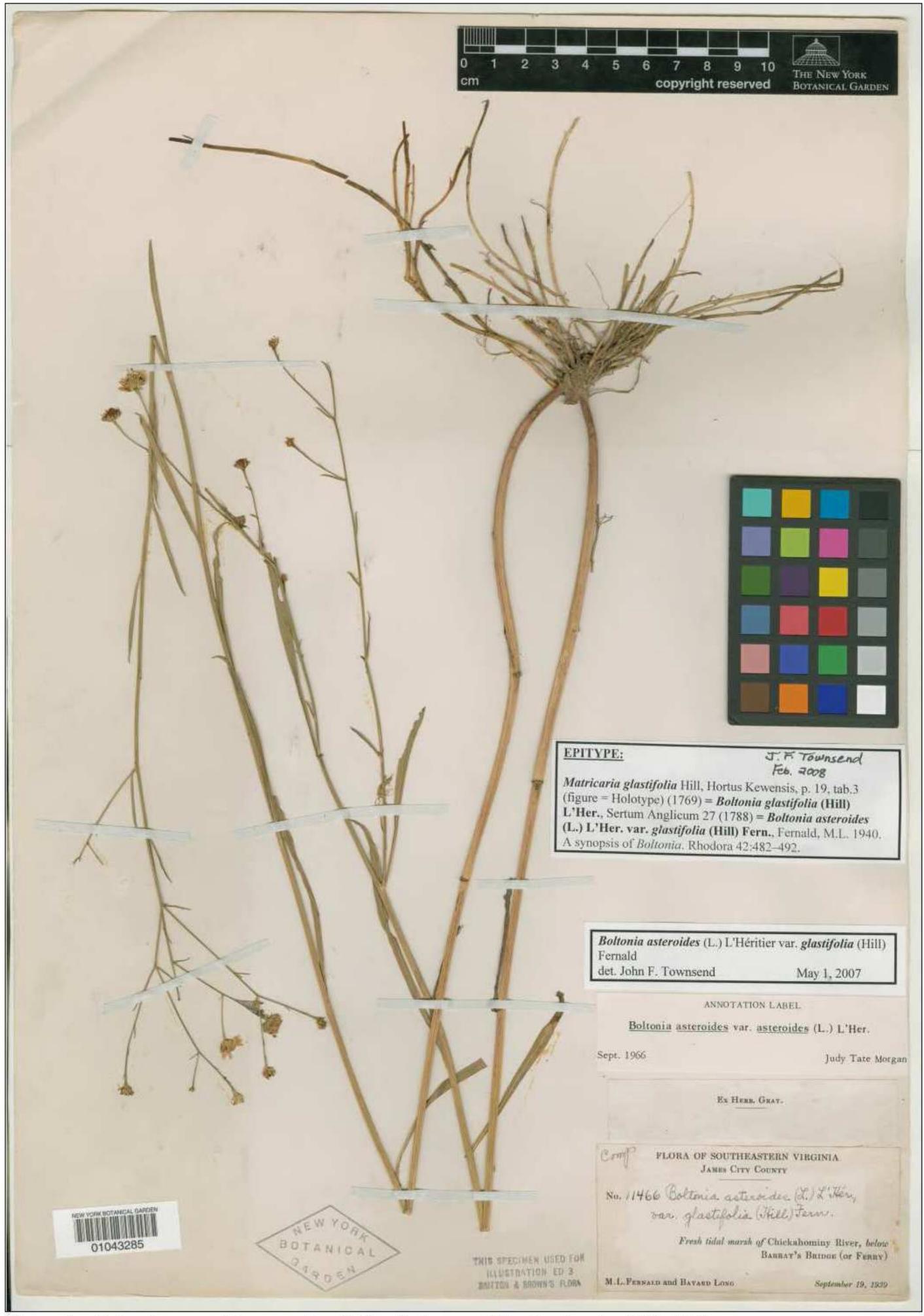


Figure 1. Boltonia asteroides var. glastifolia. Epitype of Matricaria glastifolia Hill.

Morphology of the varieties

The following discussion outlines the distinguishing morphological characteristics of var. glastifolia and contrasts this with those of var. asteroides as much as possible. Other species of Boltonia are discussed when confusion among taxa is likely or when their discussion provides a sense of context for the genus as a whole.

These observations are based upon the Boltonia holdings of NY, PH, BKL, HUH, and selected specimens from MO, GA, and LSU. General observations were also gleaned from specimens at NCU and VPI but detailed measurements were not taken.

Means of perennation

Perennial organs in *Boltonia* include roots, stolons, basal offsets, and vegetative proliferations at distal nodes. These structures are consistently found in some taxa but not others, making them useful in delimiting species boundaries, but most workers have not considered them. Fernald (1940) specifically lamented the lack of "subterranean parts" on most specimens, and declared that a proper understanding of the taxonomy of the genus depended upon intact specimens. The basal portions of Boltonia specimens are often not collected, and even when such collections are made, stolons and the long fibrous roots are easily broken off unless care is taken during excavation. In the case of the two asteroides varieties dealt with here, their means of vegetative proliferation are quite different and correlate well with other morphological characteristics.

As mentioned earlier, plants of var. glastifolia show long, prominent stolons during the flowering and fruiting period. Stolons up to 35 cm long and up to 3.5 mm thick were measured in herbarium specimens during this study. These stolons possess small, scattered, scale-like leaves along their length and are capable of producing new culms. These stolons originate anywhere from the root collar to several centimeters up the culm. In the case of the former, these structures may not be visible until the plant is excavated, while in the latter, they are readily visible in the field.

By contrast, plants of var. asteroides reproduce vegetatively by means of basal "offsets", which resemble basal leaves but are produced in the fall of the year and have the ability to become independent of the parent plant. These propagules generally consist of a slightly swollen base composed of closely imbricated leaf bases and may form adventitious roots while still attached to the parent plant. The independent nature of these propagules may even be seen in herbarium specimens, as these small plantlets can become dislodged during the collection process and may be mounted separately on the sheet. This distinctive mode of vegetative reproduction is characteristic of several other species in the genus: Boltonia apalachicolensis L.C. Anderson, Boltonia caroliniana (Walt.) Fern., Boltonia decurrens (Torr. & A. Gray) Wood, and Boltonia montana J.F. Townsend & Karaman-Castro. In the latter, propagules are also known to form at upper culm nodes.

Fernald's comparison of these two varieties only falls short in that he describes var. glastifolia as having a "... more promptly stoloniferous habit", thereby implying that var. asteroides is somewhat stoloniferous as well. This does not seem to be the case. The only mode of vegetative propagation seen in var. asteroides is the production of basal offsets as described.

Plant stature and inflorescence characteristics

Mean plant height and inflorescence size differ between var. asteroides and var. glastifolia, although the ranges overlap. In general, var. asteroides is a plant of smaller stature (mean plant ht. = 50 cm., n=36) and a little over half of its total height is composed of the plant's inflorescence (mean = 58%, n=36). Plants of var. glastifolia are larger (mean plant ht. = 92 cm., n=29), with a smaller percentage of plant height consisting of inflorescence branches (mean = 35%, n=29). Therefore, whole plants of var. asteroides are often small and compact enough to fit on an herbarium sheet with little or even no folding, while plants of var. glastifolia are nearly always folded twice or more. Since glastifolia plants often attain heights inconvenient for whole-plant collection, fragmentary specimens are common and the difference in average heights between the two taxa is probably greater than reported here. Due to the smaller size of var. asteroides and the proportionally larger size of its inflorescence, it is far more likely to have branches at or near the base than var. glastifolia.

Another noteworthy difference between these two taxa is culm orientation of the plants, which is usually erect in glastifolia (barring damage during growth) but usually ascending in asteroides. The latter taxon may only have the lowermost centimeters oriented away from the vertical, but many specimens have up to 1/2 or 2/3 of the culm oriented at least 45 degrees from the vertical. In some cases, the inflorescence branches of var. asteroides originate along a nearly prostrate culm.

In terms of the overall "look" of the plants, branch angles seen in var. glastifolia are usually fairly acute, causing these branches to be oriented in a more virgate manner than those of var. asteroides, which has branches generally emerging from the culm at a more obtuse angle. This tendency is often striking when both taxa are laid side by side, but there seems to be enough measured overlap to make this more useful as a gestalt character as anything else.

Leaf details

The leaves of var. asteroides and var. glastifolia are often distinctive in their general outline, but overlap definitely exists. Those of var. asteroides are usually elliptic to obovate with somewhat rounded to blunt apices, while those of var. glastifolia are normally acute. Those of var. asteroides are also not as markedly narrowed to the base as those of var. glastifolia. In fact, Fernald (1940) referred to the "subpetiolar bases" of var. glastifolia as characteristic of the plant. The leaf shapes seen in Fig 1 and 2 are certainly characteristic of the two varieties, but some plants do tend to posses leaves of an intermediate form, as with Fernald's (1940) plate of the taxon which shows leaves relatively intermediate between the two varieties.

In terms of leaf size and distribution, relatively little reduction in size is seen in the leaves of var. asteroides with increasing height, although one or two inconspicuous bractlets may be present near the flower heads. In many cases, the peduncles are naked or apparently so at first inspection and the whole plant seems to have leaves of generally uniform size. In contrast, the leaves of var. glastifolia are noticeably reduced with increasing height, usually diminishing most abruptly near the first inflorescence branch and continuing upwards. Characteristic of this taxon are its subulate rameal leaves, which are more numerous than in var. asteroides and are often distributed evenly along the peduncles.

Culm dimensions

Plants of Boltonia asteroides var. asteroides have narrower culms (as measured at the plant base just above presumed soil level) than var. glastifolia. As with comparisons of plant height between the two taxa, the ranges of measurements do overlap somewhat: mean = 2.25 mm. in var. asteroides (range 0.7-5.0 mm); mean = 4.8 mm. in var. glastifolia, (range 2.5-8.0 mm) but culm diameter is nevertheless useful when taken in concert with the other distinguishing characters given here. Study of specimens of both taxa indicates that this difference may be largely a function of plant height, with the generally bulkier lower stem dimension of var. glastifolia reflecting the need for more substantial support of a generally larger plant.

Habitat

The typical variety of *Boltonia asteroides* is only known from the shores and islands of the Susquehanna River downstream from Harrisburg.

The much wider-ranging var. glastifolia is strictly a Coastal Plain taxon. It is known from a more diversified set of habitats but is still restricted to well-lit situations. Populations are known to inhabit depression wetlands of various origins, wet savannas, fresh to brackish tidal marshes, as well as altered wetlands with an open canopy. All of these habitats occur on fairly acid sands, clays, mucks, and peats.

Summary

Boltonia asteroides var. glastifolia and B. asteroides var. asteroides have several character differences that argue for their separation as distinct taxa. These differences may be subtle at times and individual characters intergrade to some degree, arguing against their treatment as full species and making complete specimens and field study very valuable.

The focus of this paper has been the taxonomy and identification of members of the *Boltonia* asteroides complex, but plants of *B. asteroides* var. glastifolia from the southern USA may also be morphologically confluent with *B. diffusa* var. diffusa (pers. observ.). Generally, the plants in question are confusing due mainly to their narrower leaves, but var. diffusa has more numerous, smaller heads in a diffuse arrangement and has filiform peduncles. Other useful characters are these: the phyllaries of var. diffusa are 1.2–1.7 mm long, whereas those of asteroides var. glastifolia are 2.1–2.4 mm long, the ligules of var. diffusa are white while those of asteroides var. glastifolia are pink to white, and the capitulescence bracts (tiny "rameal leaves" subtending heads) of diffusa var difusa are less than 10 mm long and very narrow, with these small bracts making the inflorescence appear less leafy than in var. glastifolia. A number of these bracts in var. diffusa are small enough not to be evident without magnification or careful study. Lastly, the pappus awns of var. diffusa are relatively small compared to those of var. glastifolia, with Morgan (1966) reporting 0.23–0.75 mm long in diffusa and 0.89–1.01 for var. asteroides (including var. glastifolia). My own measurements suggest 0.8–1.3 mm for var. glastifolia is more appropriate.

Outward morphology of the more narrowly defined *Boltonia asteroides var. asteroides* presented here is most similar to that of *B. montana* but differs substantially in fruit morphology. The lack of cypselae wings and trichomes and dramatically reduced or absent awns in the latter taxon are thought to represent a reduced investment in dispersal structures – a trait also seen in the otherwise dissimilar *B. caroliniana* of southeastern coastal plain swamps. The apparent geographic restriction of var. *asteroides* makes it the most insular member known of the *B. asteroides* complex. However, *Boltonia apalachicolensis* was also thought to be restricted to a tight geographic area (in Florida) but specimens have since been discovered from other Gulf states (Karaman & Urbatsch 2006; Townsend, pers. observ.), so recognition of the distinguishing characteristics of var. *asteroides* may lead to the discovery of new populations of that taxon as well.

KEY TO VARIETIES OF BOLTONIA ASTEROIDES

- 1. Phyllaries linear-subulate to lanceolate; pappus awns 2/3 or less as long as the achenes, inflorescence varying from subulate-bracteate to relatively leafy; plants collectively distributed from New Jersey and Pennsylvania southward on Atlantic and Gulf coastal plains.

1. Phyllaries spatulate, oblanceolate, or linear-oblanceolate, apices cuspidate, pappus awns 2/3 or more as long as the achenes; inflorescence relatively leafy, diffusely branched; plants distributed from northeastern states through midwest to Pacific coast.

3. Phyl	laries spatulate to obovate-spatulate, membranaceous margins broad, (2) 2.5 – 6 mm wide
1-1-1-1	Boltonia asteroides var. latisquama
3. Phyl	laries oblanceolate to linear-oblanceolate, membranaceous margins narrow, 1-2.5 (-3) mm
wide	Boltonia asteroides var. recognita

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